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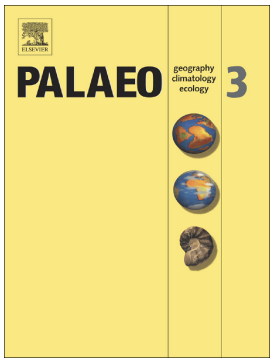


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# Late Devonian and Early Carboniferous alpha diversity, ecospace occupation, vertebrate assemblages and bio-events of southeastern Morocco

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## Abstract

The Late Devonian was a time of dramatic environmental perturbations affecting marine ecosystems. Both the Kellwasser (latest Frasnian) and the Hangenberg crises (latest Famennian) are primarily reported as phases of drastic decreases in marine diversity while the Hangenberg Crisis is also described as a bottleneck in vertebrate evolution. Fossil-bearing localities with Upper Devonian strata are of great interest to assess variations in the effects of environmental perturbations on biodiversity. For this purpose, we examined changes in alpha diversity and ecospace utilization of 21 Famennian (Late Devonian) and early Tournaisian (Early Carboniferous) invertebrate associations containing 9828 specimens from Madène el Mrakib and Aguelmous (southern Maïder Basin, northeastern Anti-Atlas, Morocco), where some layers yield exceptionally preserved gnathostome remains. Both the invertebrate and vertebrate associations contain predominantly opportunistic and pelagic taxa indicating oxygen depletion near the seafloor in this region. Nevertheless, the ecospace extension was fluctuating and correlated with regional and/or global sea-level changes and oxygenation of bottom waters. In the Maïder Basin, the ecospace was depleted after and during several bio-events such as the Kellwasser and Hangenberg crises, the *Annulata* event (middle Famennian) as well as during the early Tournaisian. Abiotic as well as biotic changes (instability of the invertebrate ecosystem) are considered to have influenced Famennian vertebrate diversity because they were more or less directly dependent on invertebrates as a food source.

**Key words**: Fossillagerstätte, Famennian, gnathostomes, invertebrates, palaeoecology, sea level

## 1. Introduction

Fundamental environmental perturbations and evolutionary changes in vertebrates and invertebrates were widely reported to have occurred during the Late Devonian (e. g. House, 1985; McGhee, 1988; Walliser, 1996; Algeo et al., 1995, 2001; Algeo and Scheckler, 1998; Caplan and Bustin, 1999; Murphy et al., 2000; Joachimski and Buggisch, 2002; Goddéris and Joachimski, 2004; Racki, 2005; Bond and Wignall, 2008; Sallan and Coates, 2010; Sallan and Galimberti, 2015; Long et al., 2015). Two biotic crises that strongly affected global biota were the Kellwasser and Hangenberg crises (Buggisch, 1991; Kaiser et al., 2006, 2008, 2015; Carmichael et al., 2015; Becker et al., 2016); in addition small-scale events such as the Condroz (Becker, 1993), *Annulata* (Becker and House, 1997, 2000; Sandberg et al., 2002; Korn, 2004; Racka, 2010; Hartenfels and Becker, 2016a) and Dasberg events (Hartenfels and Becker, 2009; Hartenfels, 2011; Kaiser et al., 2011) have been recognized in Frasnian and Famennian successions (House, 1985, 2002; Walliser, 1996; Table 1). Both the Kellwasser Crisis (latest Frasnian) and the Hangenberg Crisis (end-Devonian) caused severe losses of global diversity of many marine and terrestrial biotic groups (Newell, 1952, 1956, 1963; Raup and Sepkoski, 1982; McGhee, 1996, 2001, 2014; Alroy, 2010; McGhee et al., 2013; Sallan and Coates, 2010; Friedman and Sallan, 2012; Sallan and Galimberti, 2015). However, causes for ecosystem changes and diversity loss during the Late Devonian are still highly debated (e.g. Buggisch, 1991; Algeo et al., 1995, 2001; Algeo and Scheckler, 1998; Sandberg et al., 2002; Riquier et al., 2006; Long et al., 2015) and concerning vertebrates, this time interval was mainly studied via global diversity curves (e.g. Sallan and Coates, 2010; Friedman and Sallan, 2012; Sallan and Galimberti, 2015). Therefore, a regional study on the vertebrate ecosystem including other organisms such as invertebrates from a locality with detailed stratigraphical and sedimentological information is needed. The Maïder Basin of the eastern Anti-Atlas is suitable for this purpose.

**Table 1.** Summary of possible causes and effects of Famennian (Late Devonian) and Tournaisian (early Carboniferous) bio-events and environmental perturbations.

| **Bio-event/ Environmental changes** | **Causes** | | **Effects** | |
|---|---|---|---|---|
| | **regional: Maïder** | **global** | **regional: Maïder** | **global** |
| **Kellwasser (end-Frasnian)** | -dysaerobic condition<br>-high sea level stands<br>(Wendt & Belka, 1991) | - anoxia<br>- sea-level changes<br>- drop in selenium level<br>(e.g. Buggisch 1990; Sandberg et al., 2002; Bond et al., 2004; Gereke & Schindler, 2012; Long et al., 2015) | - Kellwasser facies rich in fossils<br>(Wendt & Belka 1991) | -Loss in marine biodiversity<br>(e.g. McGhee, 2014) |
| **Condroz (early Famennian)** | -regression<br>(Wendt & Belka, 1991; Becker, 1993) | -regression<br>(Becker, 1993; Becker et al., 2012) | - extinction of few ammonoid genera<br>(Becker, 1993) | - extinction of few ammonoid genera<br>(Becker, 1993) |
| ***Annulata* (middle Famennian)** | - hypoxia to anoxia, dysoxic<br>- transgression<br>(Hartenfels 2011; Hartenfels & Becker 2016) | - anoxia<br>- transgression<br>(Walliser, 1996; House, 1985; Sandberg et al., 2002; Joachimski et al., 2009; Becker 1992; Hartenfels & Becker 2005; Racka 2010) | - mass occurrence of the ammonoid *Platyclymenia*<br>-Small-scale extinction in ammonoids<br>(Korn, 2004; Hartenfels & Becker 2016) | - mass occurence of the ammonoid *Platyclymenia*<br>-Small-scale extinction<br>(Korn, 2004) |
| **Dasberg (late Famennian)** | -hypoxic conditions<br>-two transgressive events<br>(Hartenfels & Becker 2009; Hartenfels 2011) | - regional blackshales<br>- transgression<br>(House, 1985; Hartenfels & Becker 2009) | - species level extinction<br>(Becker, 1993; Hartenfels & Becker, 2009, Kaiser et al., 2015) | - coincides with environmental changes<br>(Hartenfels & Becker 2009) |
| **Hangenberg (end-Famennian)** | - anoxia<br>- transgression followed by a regression<br>(Kaiser et al., 2011, 2015) | - anoxia<br>- global cooling<br>- regression<br>- transgression followed by a regression<br>- eutrophication<br>- drop in selenium level<br>(e.g. Caplan & Bustin, 1999; Algeo and Scheckler, 1998; Kaiser et al. 2006; Carmichael et al., 2015) | - extinction in invertebrate groups (mostly ammonoids, trilobites, rhynchonellid brachiopods, bivalves, rugose corals) and in early gnathostomes (arthodires, chondrichthyans)<br>(Korn et al. 2004; Kaiser et al., 2011) | - Loss in marine biodiversity<br>- bottleneck in vertebrates<br>(e.g. Sallan and Coates, 2010; Friedman and Sallan, 2012; Sallan and Galimberti, 2015) |
| **Alum Shale (lower-middle Tournaisian)** | - anoxia<br>- transgression<br>(Kaiser et al., 2011) | - anoxia<br>- transgression<br>(Becker, 1993; Johnson et al., 1985; Siegmund et al., 2002) | -ammonoids: species level extinction<br>(Kaiser et al., 2015; see also Korn et al., 2002, 2007; Becker et al., 2006; Ebbighausen & Bockwinkel, 2007) | -Some groups (corals, trees, fish) affected by the Hangenberg Crisis, diversified only after the Alum Shale Event.<br>(Poty, 1999; Decombeix et al., 2011; Denayer et al., 2011; Kaiser et al., 2015) |

The eastern Anti-Atlas of Morocco is well-known for its highly fossiliferous outcrops of Devonian marine sedimentary rocks. In recent years (e.g., Klug et al., 2008, 2016), some stratigraphic intervals of several localities became known for their Fossillagerstätten qualities because of the abundance ("Kondensat-Lagerstätte") and exceptional preservation of fossils ("Konservat-Lagerstätte" *sensu* Seilacher, 1970). Among those, Madène El Mrakib (Maïder Basin; cf. Wendt, 1985; Wendt and Belka, 1991; see Fig. 1, Fig. 3) became famous for its wealth and diversity of remains of well-preserved invertebrates such as cephalopods (Petter, 1959, 1960; Korn, 1999; Becker, 1995, 2002; Becker et al., 2000, 2002; Korn and Klug, 2002; Klein and Korn, 2014; Korn et al., , 2014, 2015a, b, 2016a, b; Hartenfels and Becker, 2016a, b; Klug et al., 2016; Korn and Bockwinkel, 2017), crinoids (Klug et al., 2003; Webster et al., 2005), brachiopods (Sartenaer, 1998, 1999, 2000) and trilobites (Struve, 1990). Vertebrate macroremains are rather rare in most Devonian strata of Morocco, but they become more abundant in sediments of Late Devonian age. Particularly, three-dimensionally preserved remains of various Late Devonian (Frasnian and Famennian) species, mostly of placoderms, from the eastern Anti-Atlas have been described during the last decades (Lehman, 1956, 1964, 1976, 1977, 1978; Lelièvre and Janvier, 1986, 1988; Lelièvre et al., 1993; Rücklin, 2010, 2011; Rücklin et al., 2015; Rücklin and Clément, 2017). Remains of other gnathostome groups such as actinopterygians, acanthodians and chondrichthyans are restricted to microremains, fin spines or isolated jaws (Termier, 1936; Lehman, 1976; Derycke, 1992; Hampe et al. 2004; Derycke et al., 2008; Ginter et al., 2002; Klug et al., 2016; Derycke, 2017). In several middle Famennian layers of the Maïder Basin, we recently discovered new, often articulated skeletons of gnathostomes such as placoderms, actinopterygians, sarcopterygians and chondrichthyans, which will strongly improve the knowledge of this Devonian Konservat-Lagerstätte and thus the palaeoenvironment of this small marine basin.

In order to better understand Late Devonian ecosystems of the Maïder through time, we studied alpha diversity and palaeoecology of the gnathostomes and invertebrates of a series of

sufficiently fossiliferous strata. Our aim is to answer the following questions: (1) How did the ecosystem change during the Famennian in the Maïder? (2) Which groups of gnathostomes were present in the assemblages and were their occurrences related to invertebrate diversity? (3) What were the effects of global ecological changes and events on the composition and fluctuations in these assemblages?

## 2. Material and Methods

### 2.1 Geological setting

Konservat-Lagerstätten conditions prevailed in wide areas of the Maïder Basin (northeastern Anti-Atlas, Morocco) during the Famennian (Fig. 1); only south of Tafraoute, exceptionally preserved fossils have not been found yet. We discovered two layers containing exceptionally preserved vertebrate fossils, particularly chondrichthyans, in the Maïder: The middle Famennian (*Maeneceras* horizon) phyllocarid layer, named after its high abundance of phyllocarids, contains most of the gnathostome remains preserved in ferruginous nodules while in the second layer (early-middle Famennian) fewer remains were found so far (Fig. 2). A third layer with prevailing Konservat-Lagerstätten conditions (latest Famennian, Hangenberg Black Shale equivalent) bearing mostly macroinvertebrates and rarely acanthodian teeth has recently been documented by Klug et al. (2016).

The phyllocarid layer crops out at various localities such as Bid er Ras, Jebel Oufatene, Mousgar, Tizi Mousgar, Aguelmous Azizaou, Oued Chouairef, Tizi n`Aarrat Chouiref and Madène El Mrakib (Fig. 1). However, in many of these localities, the sedimentary succession of the Famennian strata is partially covered by scree, often delivered from the overlying massive sandstone of the Fezzou Formation which is an equivalent to the Hangenberg Sandstone of the Tafilalt (Kaiser et al., 2011; Klug et al., 2016). The Famennian succession is best exposed at Madène el Mrakib in the southern Maïder because of large scale folding and

erosion towards the Maïder Valley and Tafraoute. Therefore, we measured a section at this locality from strata of latest Frasnian age ("Upper Kellwasser Event") up to the Hangenberg Black Shale equivalent (Rücklin, 2010, 2011; Klug et al., 2016).

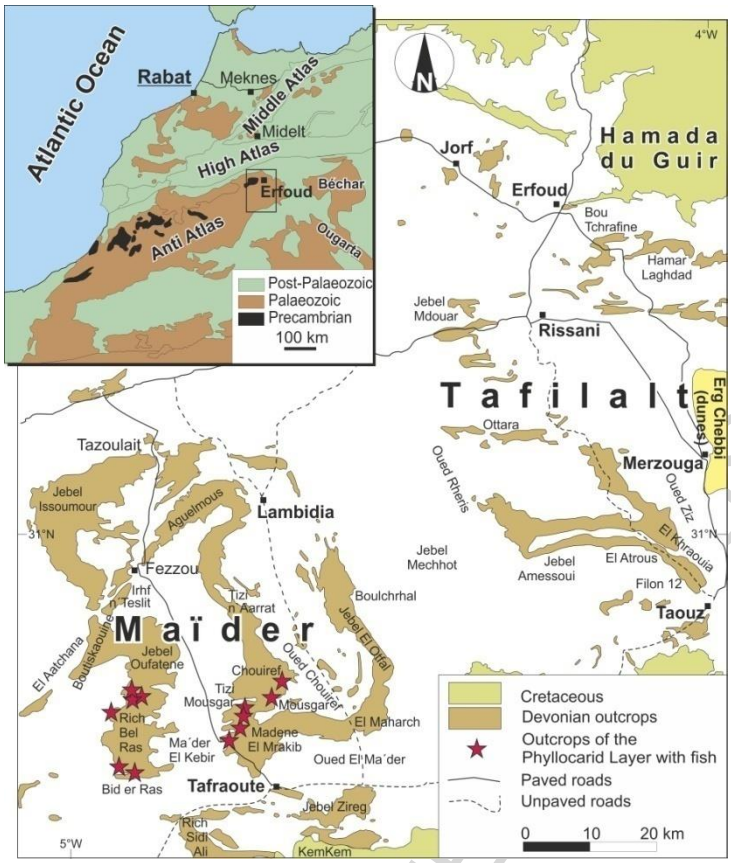


**Fig. 1.** Geological map of the Maïder and Tafilalt region in the eastern Anti-Altas of Morocco. Localities with phyllocarid layer containing well-preserved remains of gnathostomes are marked here; faunal changes have been studied from lower to upper Famennian at Madène el Mrakib and from lower to middle Tournaisian at Aguelmous. New data about vertebrate diversity has been compared to the locality Filon 12 of the Tafilalt region.

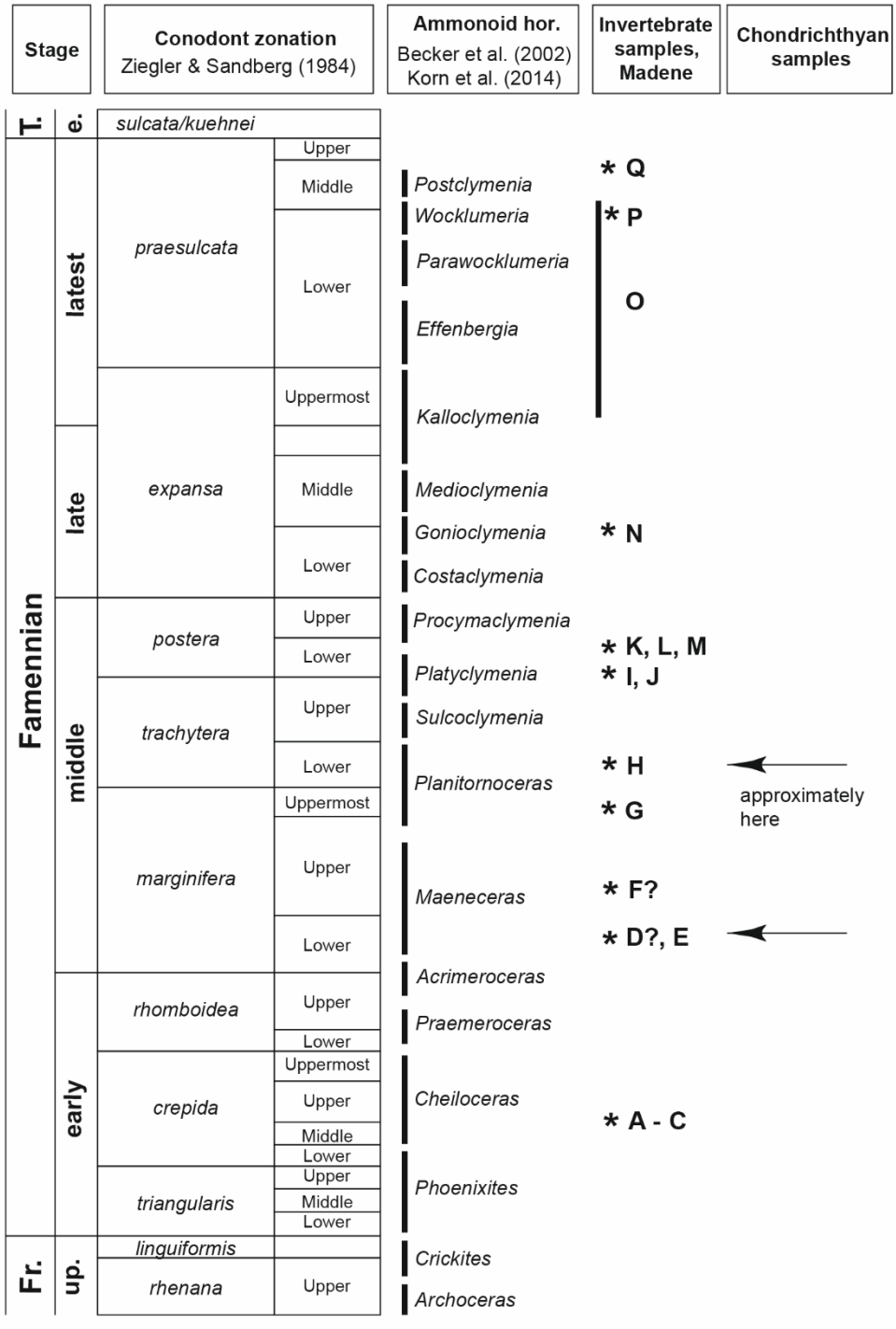


**Fig. 2.** Positions of the Famennian samples collected from Madène el Mrakib within the global and regional condodont zonations (Ziegler and Sandberg, 1984 and Hartenfels, 2011) and ammonoid horizons (Becker et al. 2002; Korn et al., 2014). Asterisks and bars mark the approximate position of the samples.

## 2.2 Collection of alpha diversity data

Twelve successive fossil assemblages containing 3591 specimens of macroinvertebrates (Figs. 3, 4A: associations A-I, K, P-Q; Table S1) co-occurring with gnathostome remains were collected from the Famennian of Madène el Mrakib to examine changes in alpha diversity and palaeoecology. To achieve an adequate resolution in species abundance and composition and to reduce biases from differences in sample size, only horizons yielding at least 100 specimens were sampled. Most associations contain numerous formerly pyritized specimens (now limonitic and haematitic caused by deep weathering of the sediments) whereas other associations are preserved in limestone nodules, sideritic nodules and marly beds. In the latter case, specimens were counted in situ on a bedding plane, depending on the outcrop conditions. To complement our data, we examined 3458 specimens of three middle Famennian (*Platyclymenia* and *Procymaclymenia* horizons) and two late Famennian (*Gonioclymenia* to *Wocklumeria* horizons) samples from Madène el Mrakib that are housed in the Museum für Naturkunde in Berlin (Fig. 2: associations J, L-O; Table S1; biozonation is figured in Korn et al., 2014). This material contains mostly ammonoids and was published by Korn et al., (2014, 2015a). In addition to the Famennian samples A to Q from Madène, we examined four samples R to U (Table S1) containing another 2779 specimens of Early to Middle Tournaisian (Early Carboniferous) age from Aguelmous. The ammonoids of these samples were published by Ebbighausen and Bockwinkel (2007).

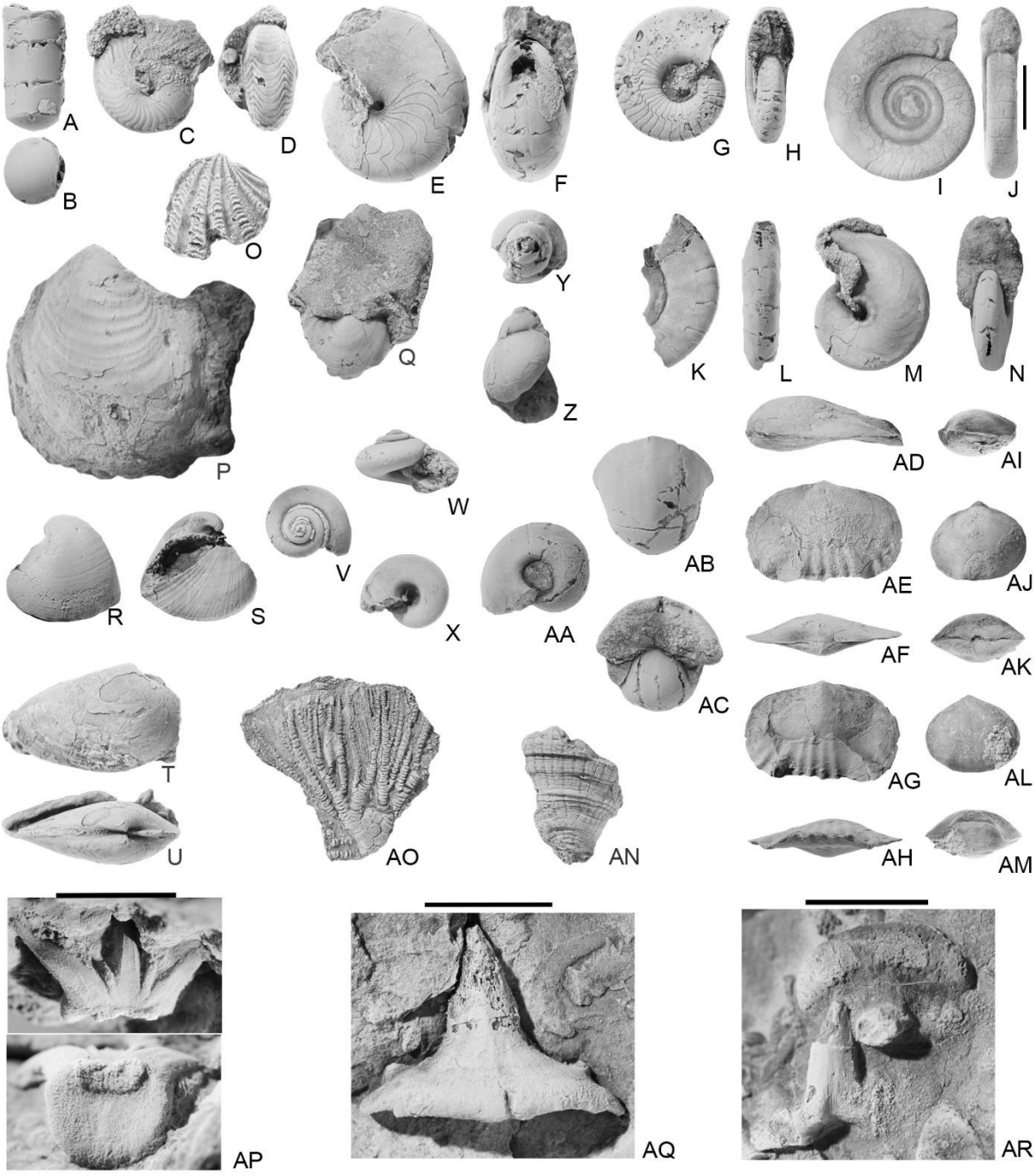


**Fig. 3**. Famennian invertebrate and gnathostome remains from the Maïder. A – B – *Bactrites* sp., lateral and septal view, x 2, PIMUZ 34012. C – D – *Falcitornoceras falciculum*, lateral and ventral views, x 3, PIMUZ 34014. E – F – *Ch.* (*Staffites*) *afrispina*, lateral and ventral views, x 1, PIMUZ 34015. G – H – *Planitornoceras pugnax*, lateral and ventral views, x 2, PIMUZ 34013. I – J – *Platyclymenia annulata*, lateral and ventral views, x 1, PIMUZ 34010. K – L – *Pseudoclymenia* sp., lateral and ventral view, x 1.5, PIMUZ 34011. M – N – *Aulatornoceras* sp., lateral and ventral view, x 1.5, PIMUZ 34016. O – *Glyptohallicardia* sp., lateral view, x 2,

PIMUZ 34017. P – *Prosochasma* sp., lateral view, x 0.75, PIMUZ 34018. Q – *Guerichia* sp., lateral view, x 3, PIMUZ 34019. R – S – *Loxopteria* sp., lateral views, x 1, PIMUZ 34020. T – U – *Paleoneilo* sp., lateral and dorsal view, x 2, PIMUZ 34021. V – X – undetermined gastropod, apical, apertural and basal view, x 2, PIMUZ 34022. Y – Z – undetermined gastropod, apical and apertural view, x 2, PIMUZ 34023. AA – AC – undetermined bellerophontid, lateral, dorsal and apertural view, x 2, PIMUZ 34024. AD – AH – *Phacoiderhynchus antiatlasicus*, lateral, dorsal, posterior, ventral and anterior views, x 0.75, PIMUZ 34025. AI – AM – undetermined brachiopod, lateral, dorsal, posterior, ventral and anterior views, x 1, PIMUZ 34026. AN – Rugose coral, lateral view, x 1.5, PIMUZ 34027. AO – *Moroccocrinus ebbighauseni*, lateral view, x 1, PIMUZ 34028. AP –*Phoebodus* sp., labial and aboral view, scale bar = 5 mm, PIMUZ A/I 4656. AQ – cladodont shark tooth, lingual view, scale bar = 10 mm, PIMUZ A/I 4657. AR – cladodont shark tooth, labial and oral view, scale bar = 5 mm, PIMUZ A/I 4658.

The ages of the associations were determined by ammonoids (cf. Korn, 1999; Becker et al., 2002; Korn et al., 2014). For some associations (A-C, E, G-U in Table S1), a correlation between ammonoid horizons and conodont zones was possible (Fig. 2; Hartenfels 2011). The conodont biozonation of the Famennian was recently revised (Kaiser et al., 2009; Spalletta et al., 2017). However, for the correlation of our data to global and regional sea level curves (Wendt and Belka, 1991; Haq and Schutter, 2008; Kaiser et al., 2011), we used the previous conodont zonation of Sandberg et al. (1978) and Ziegler and Sandberg (1984).

The fossils were determined at species level wherever possible and subsequently, the relative abundance of every taxon was calculated and plotted as histograms per association. Moreover, the trophic nucleus concept of Neyman (1967) was applied to our abundance data to detect taxa that were dominating each fauna. The trophic nucleus includes taxa whose relative abundances contribute to 80 % of the total abundance of all taxa of a fauna. Additionally to the analysis of the alpha diversity of complete samples, we counted ammonoid genera of every association because some middle and upper Famennian samples

exclusively contained cephalopods when considering macrofossils only. In order to compare samples of different sample sizes and to avoid biases caused by different methods or by varying sampling efforts to each other, we rarefied the abundance data of each fauna with the software package PAST (Hammer et al., 2001).

### 2.3 Ecospace occupation

Analyses in palaeoecology are based on the theoretical ecospace concept *sensu* Bush et al. (2007). We grouped all taxa according to ecological categories of 'tiering', 'motility' and 'feeding mechanism'. The combination of these three ecological parameters leads to a unique three-dimensional mode of life per taxon. 'Tiering' categorises the position of organisms in the water column such as pelagic, erect, surficial, semi-infaunal and shallow or deep infaunal. We assigned all cephalopods such as ammonoids, bacritids and orthocerids to a pelagic lifestyle. The habitat of fossil phyllocarid crustaceans is still a matter of debate. Due to the ferruginous sediments (probably due to pyrite weathering; the pyrite points at low oxygen conditions) in the Maïder Basin, we assigned the phyllocarids to a nektobenthic or pelagic mode of life as it was proposed before by several authors (e. g. Siveter et al., 1991; Vannier and Abe, 1993; Zatoń et al., 2013). Nevertheless, it has to be considered that recent benthic phyllocarids are able to survive short-term anaerobic conditions and that this tolerance might have existed in extinct taxa as well (Vannier et al., 1997). Besides the crinoid *Moroccocrinus ebbighauseni* that was probably pseudoplanktonic in early to middle ontogenetic stages and perhaps benthic in adult stages (Klug et al., 2003; Webster et al., 2005), we found one specimen of a crinoid holdfast in one of the associations, which might be benthic and erect (unless it was attached to a living ammonoid). All gastropods (*Macrochilina*), amphigastropods (*Bellerophon*), brachiopods (rhynchonellids, *Aulacella*), rugose corals and trilobites in the samples inhabited the sediment surface (Bush et al., 2007). Cladochonid-type tabulate corals (Webster et al., 2005) are lacking in our samples of Madène el Mrakib. The

lifestyle of bivalves is highly diverse and it is still not completely clarified for all fossil taxa. Species of the genera *Guerichia, Prosochasma, Opisthocoelus, Ptychopteria* and *Streblopteria* were probably living on the sediment surface (Amler, 1996, 2004, 2006). Amler (2004) assumed that small bellerophontids, gastropods and the bivalve genus *Guerichia* could have lived on erect benthic or floating algal thalli and therefore, their occurrence was not limited to the sea floor (oxygen-poor conditions cannot be ruled out). We determined these organisms as surficial because we found only little organic matter in our section and the habitat might have been too deep for large benthic algae (estimated depth at Madène el Mrakib is around 200 m and therefore below the euphotic zone; Tessitore et al. 2016). Epibenthic to semi-infaunal lifestyles were proposed for the bivalve *Buchiola* (*Buchiola*) and *Glyptohallicardia* (Grimm, 1998) whereas *Loxopteria* might have been semi-infaunal (Nagel, 2006). *Paleoneilo* and *Metrocardia* as well as lingulid brachiopods have been suggested to be shallow infaunal based on actualistic comparisons (Thayer and Steele-Petrovic, 1975; Amler, 1996; Kříž, 2004). Bivalve species that we could neither determine nor assign to modes of life, we summarized as 'benthic organism' in a separate category.

'Motility' refers to locomotory capabilities of organisms such as freely, fast or slow motile, attached or non-attached facultatively motile or completely non-motile. We assigned phyllocarids and trilobites to freely, fast motile organisms (Vannier et al., 1997; Fortey, 2004), whereas cephalopods and gastropods were rather slow motile organisms (Westermann, 1999; Westermann and Tsujita, 1999). Rugose corals, crinoids, brachiopods and the bivalve genera *Guerichia*, *Ptychopteryia* and *Streblopteria* were non-motile organisms attached to their substrate whereas *Prosochasma* and *Opisthocoelus* were attached as well but facultatively motile (Bush et al., 2007; Amler, 1996, 2004; Nagel, 2006; Kříž, 2004). Buchiolid bivalves were sessile and unattached (Grimm, 1998).

'Feeding mechanism' describes whether animals acquire food by predation, mining, grazing suspension filtering or deposit feeding. For cephalopods, we assume this group to be

microphagous predators (Klug and Lehmann, 2015). Brachiopods, rugose corals, crinoids and most bivalves were suspension feeders (*Paleoneilo* represents a deposit feeder; Amler, 2004) while gastropods were assigned to grazers. The phyllocarids of the Maïder were suspension feeders as they were probably pelagic due to the dysoxic sediments and poor benthic bottom life. Trilobites had a high variety in acquiring food including feeding on plankton and organic particles, scavenging or preying on small organisms on or near the bottom (Fortey and Owens, 1999; Fortey, 2004). On the one hand, the trilobites in our sample were rather small benthic forms that possibly were deposit feeding. On the other hand, they look morphologically similar to forms (e. g. big eyes for good vision, Fortey, 2004) that were scavengers or also microphagous predators.

## 3. Results

### 3.1. Fluctuations in invertebrate diversity

In total, the 21 associations contain 9828 specimens that were assigned to around 227 species (Tables S1, S3). Since we separately analyzed ammonoids and the complete assemblages of selected layers, the entire assemblage is concerned when we write of species; ammonoid diversity is separately depicted and indicated. During the early Famennian (*Cheiloceras* horizon), the general species richness increases from three up to twelve species and one to five ammonoid genera were counted within this interval (Figs. 4A: association A-C; 5A-C). The middle Famennian phyllocarid layer (*Maeneceras* horizon) contains numerous gnathostome remains (Figs. 4: association E; 5E) and eight species of invertebrates including two ammonoid genera. In the following middle Famennian associations (*Maeneceras* to *Planitornoceras* horizon), 11 to 14 species and one to four ammonoid genera were present (Figs. 4A, associations F-H; 5F-H). We found two cephalopod species and one ammonoid genus in the *Annulata* Black Shales (middle Famennian, *Platyclymenia* horizon) whereas in

the subsequent sample, 24 ammonoid species and five ammonoid genera were counted (Figs. 4I, 7, Table S1: association I-J). In the following sample above the *Annulata* Black Shales, species richness reaches 22 species comprising six ammonoid genera (Fig. 4A: association K; 5J). In the two other samples of the middle Famennian (*Platyclymenia/ Procymaclymenia* horizon), thirteen and nine species were counted and in both samples, seven ammonoid genera were present (Fig. 7: associations L-M). In the latest Famennian (*Gonioclymenia* to *Wocklumeria* horizons), 13 species including seven ammonoid genera and three species including one ammonoid genus were counted (Fig. 7: association N-O). Nine taxa were found so far in the *Wocklumeria* horizon (latest Famennian; however, these layers are not yet sufficiently sampled to provide accurate abundance data (Figs. S1, 4A: association P). In the Hangenberg Black Shale equivalent (latest Famennian), eleven species containing four ammonoid genera were found (Figs. 4A, association Q; 5K). The earliest Tournaisian association (Fig. 6A) is diverse containing 32 species (thereof eight ammonoid genera) while the other three Tournaisian associations contained eight to fifteen species including two to seven ammonoid genera (Fig. 6B-D; Table S1, association R-U).

We estimated the sampling bias caused by differences in the method and duration of sampling by rarefaction analysis. The rarefaction curves describe the number of taxa that could have been collected with extending the sampling duration (increasing number of specimens). Some graphs show steep curves that mean more taxa would have been found with further collecting within some of the samples (Figs. S2, S3). However, the biased samples still show low species numbers compared with the most diverse samples regarding the species numbers that could have been found within a certain number of collected specimens (we checked for 90 specimens in each graph). Therefore, trends in diversity are not strongly biased and here considered reliable; nevertheless, it cannot be ruled out that these results are influenced by faunal mixing to a small extend (e.g., Kidwell and Bosence, 1991); indicators

for strong condensation, such as eroded and reworked fossils, very reduced thickness, extensive hiatuses and iron crusts, are absent.

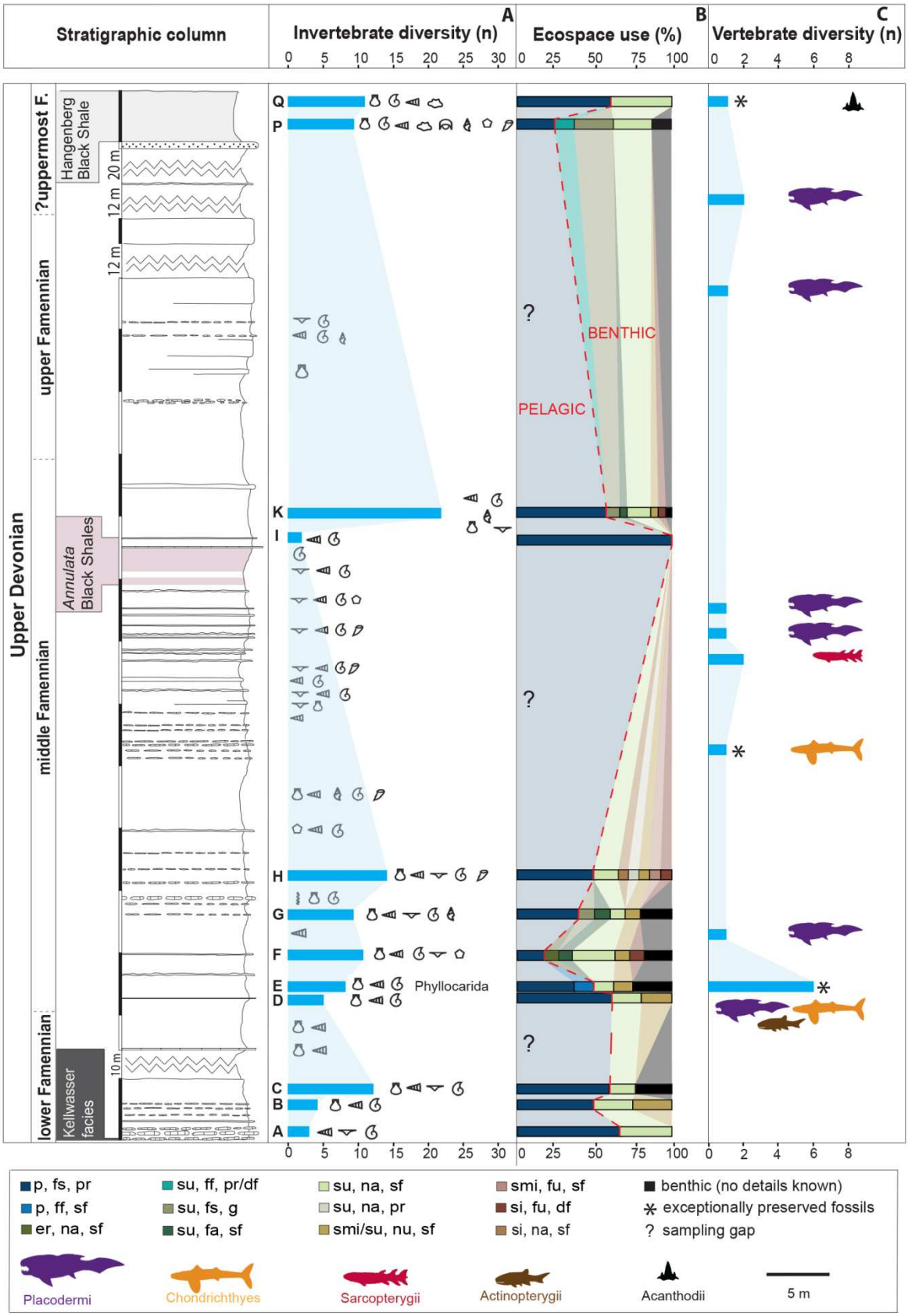

**Fig. 4.** Changes in diversity and ecospace use during the Famennian at Madène el Mrakib. A – Histograms represent the number of species per association and the changes in diversity (Table S1). Intervals without histograms often contained rare and/or weathered and compressed fossils which were mostly impossible to determine to the species level. These intervals were not included in the analysis as they would have resulted in biased species numbers. B – Ecospace expansion (ecological classification after Bush et al., 2007) shows change in the number of three-dimensional modes of life along the section. C – Changes in gnathostome diversity and composition. Abbreviations of ecological categories: Tiering – p: pelagic, er: erect, su: surficial, smi: semi-infaunal, si: shallow infaunal; Motility – ff: freely fast, fs: freely slow, fu: facultative unattached, fa: facultative attached, nu: non-motile and unattached, na: non-motile and attached; Feeding mechanism – sf: suspension feeder, df: deposit feeder, g: grazer, pr: predators.

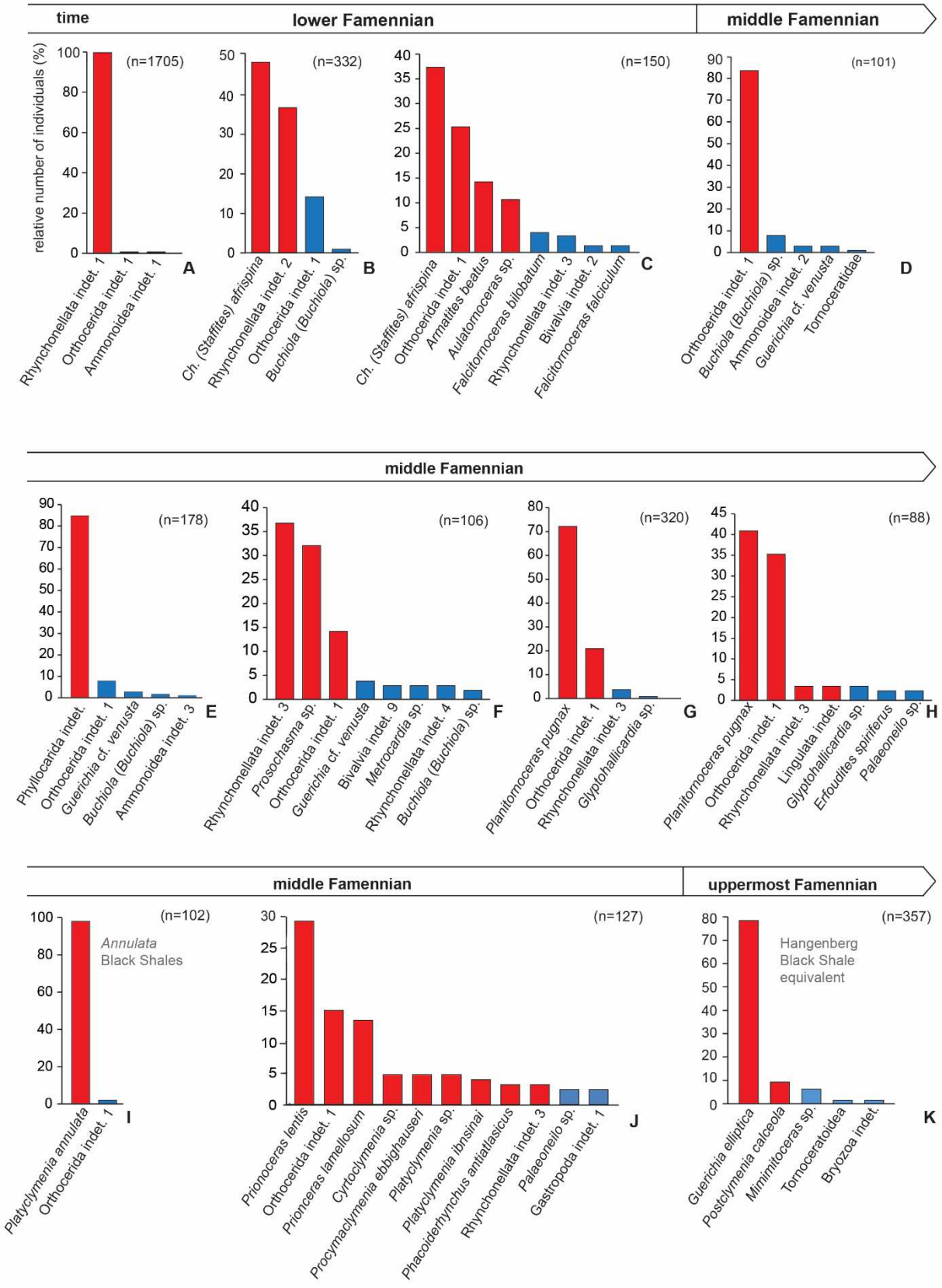


**Fig. 5.** Species abundances of 11 successive faunal samples of early to late Famennian age from Madène el Mrakib in the Maïder region (Morocco); red bars represent the dominant species of each association. A – association A, early Famennian, all three sampled taxa are shown. B – association B, early Famennian, all four

sampled taxa are shown here. C – association C, early Famennian, nine of thirteen taxa are shown . D – association D, middle Famennian, all five sampled taxa are shown here. E – association E, middle Famennian, five of eight taxa are shown here. F – association F, middle Famennian, eight of eleven taxa are shown here. G – association G, middle Famennian, four of nine taxa are shown here. H – association H, middle Famennian, seven out of fourteen taxa are shown here. I – association I, middle Famennian, *Annulata* event layer, all two sampled taxa are shown here. J – association K, middle Famennian, 11 out of 22 sampled taxa are shown here. K – association Q, late Famennian, Hangenberg Black Shale, five out of eleven sampled taxa are shown here. Not depicted species are listed in Table S3.

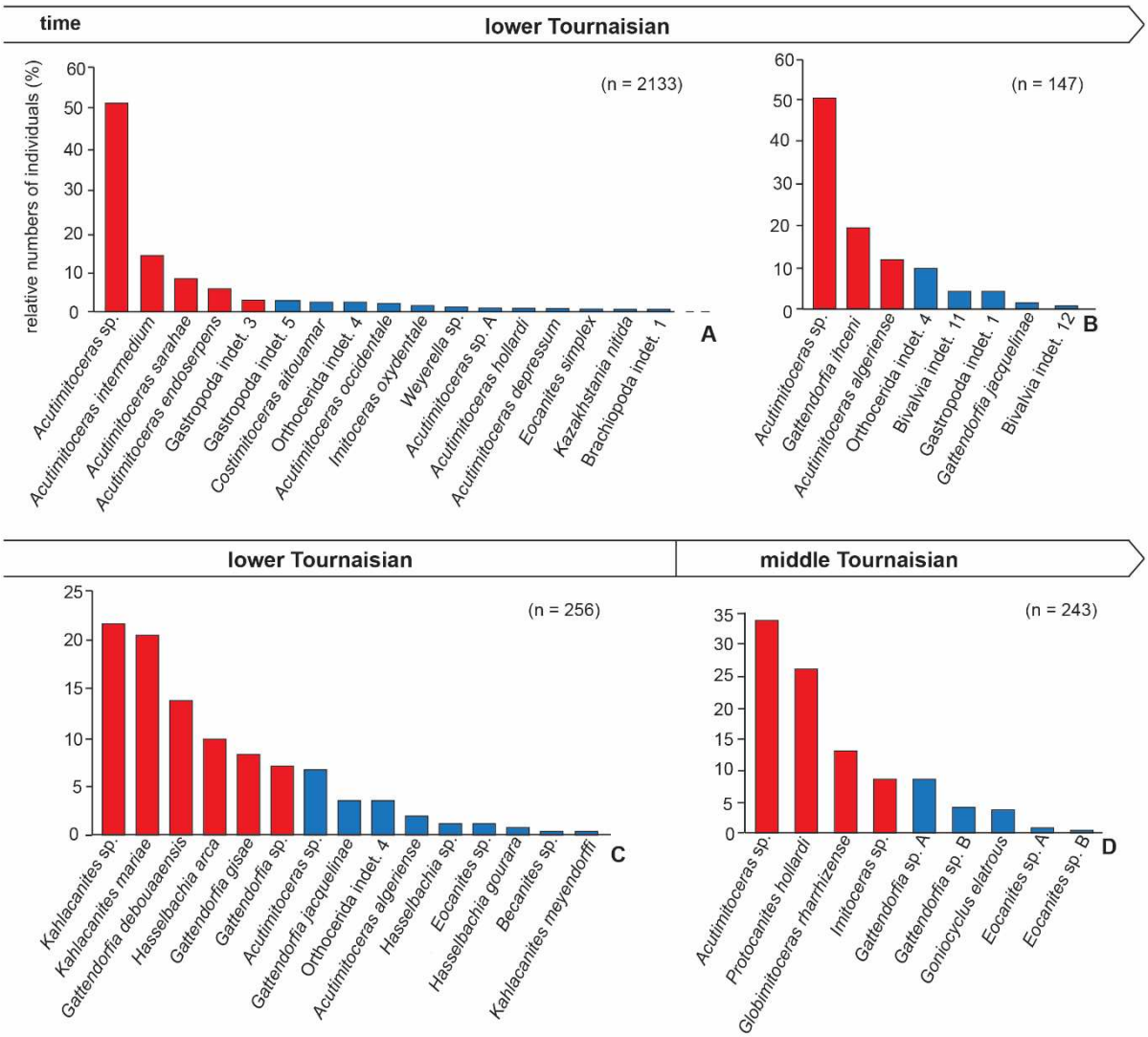


**Fig. 6.** Abundances of species and faunal composition of early and middle Tournaisian associations from Aguelmous (Maïder region); data and bed numbers were taken from the collection of Ebbighausen & Bockwinkel (2007); red bars represent dominant taxa. A – association R, early Tournaisian association, 17 out of

32 sampled taxa are shown here. B – association S, early Tournaisian association, all eight sampled taxa are shown here. C – association T, early Tournaisian association, all 15 sampled taxa are shown here. D – association U, middle Tournaisian association, all the nine sampled taxa are shown here. Not depicted species are listed in Table S3.

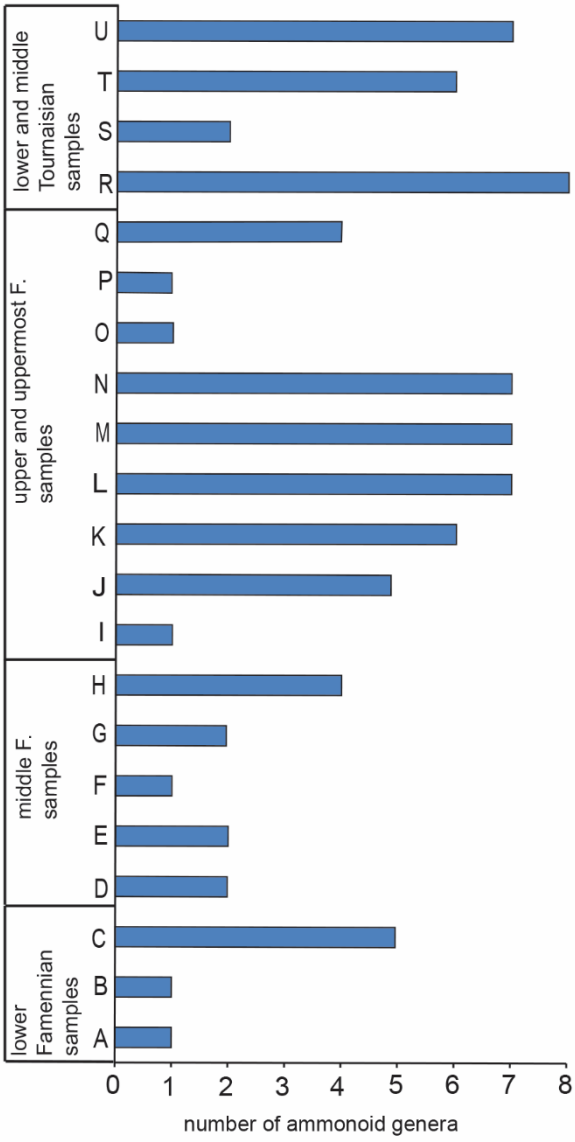


**Fig. 7.** Number of ammonoid genera per association. Associations A-Q were collected from the Famennian of Madène el Mrakib, associations R-U were sampled from the Tournaisian of Aguelmous.

### 3.2. Changes in the trophic nucleus

Cephalopods such as ammonoids and orthocerids are the most important components of the trophic nucleus in some early, middle and late Famennian samples (Fig. 5B, 5F, 5H, 5J) or

were even the only dominant group (Fig. 5C-D, 5G, 5J). Phyllocarids occur only in one sample but in great abundance and thus are dominant at Madène el Mrakib (Fig. 5E). Brachiopods and bivalves contributed rarely to the trophic nucleus except for in a middle Famennian sample and in the Hangenberg Black Shale equivalent (Fig. 5A, 5F, 5H). In the Tournaisian associations, ammonoids mainly constitute the trophic nucleus except for one single gastropod species that is present in the oldest Tournaisian association (association R in Fig. 6A).

### 3.3. Ecospace occupation during the Famennian

In the early Famennian (*Cheiloceras* horizon) associations, two to three modes of life were present and pelagic lifestyles had higher relative abundance than benthic lifestyles (67 versus 33 %; Fig. 4B; association A-C). The middle Famennian phyllocarid layer (*Maeneceras* horizon) contains taxa dominated by pelagic lifestyles and taxa with an additional mode of life (freely pelagic, fast motile deposit feeders that are represented by phyllocarids) was found. By contrast, the next younger association yielded a high relative abundance of benthic modes of life (82 %), which stays high (46-68 %) in the following middle Famennian associations (F-H). The association of the *Annulata* Black Shales represents only pelagic modes of life, while the association above the *Annulata* Black Shales (*Platyclymenia/ Procymaclymenia* horizon) contains seven modes of life represented by benthic and pelagic organisms (freely pelagic, slow-motile predators having the highest abundance, 57%). In the latest Famennian (*Gonioclymenia* to *Wocklumeria* horizon), pelagic, freely motile predators were highly abundant (92 %). However, samples were biased towards cephalopods and therefore, they were excluded from this analysis. The *Wocklumeria* horizon (latest Famennian age, association P) contained organisms of four modes of life and benthic organisms had a high relative abundance (75 %) in comparison to pelagic forms (25%). In the

following Hangenberg Black Shale equivalent (association Q), only two modes of life were present of which the pelagic organisms had the highest abundance (60%). During the Early Tournaisian, the ecospace of associations R and S (Aguelmous, Fig. 9C) consists of five modes of life but in the following two associations (Fig. 9C: associations T and U), the ecospace is reduced to one single mode of life. In all the Tournaisian associations, pelagic organisms are more abundant than benthos.

In total, we report here 12 or possibly 13 modes of life (some bivalves could not be assigned to certain three-dimensional lifestyles) from 216 theoretically possible combinations. This value lies below the middle Palaeozoic (Late Ordovician to Devonian) value of about 21 modes of life known from North America and Europe (Bush et al., 2007). Nineteen modes of life were recorded in the Early Devonian strata of the Tafilalt region (Jebel Ouaoufilal, Filon 12, see Fig. 1) that is palaeogeographically and temporally closer situated to the Late Devonian of the Maïder (Frey et al., 2014). The slightly impoverished Late Devonian ecological diversity of the southern half of the Maïder Basin points at unfavorable living conditions that coincide with the occurrence of reddish ferruginous deposits indicating dysoxic environmental conditions (Korn, 1999; Korn et al., 2015b; Kaiser, 2005; Webster et al., 2005).

### 3.4. Diversity and ecospace use in vertebrates

Skeletal remains of chondrichthyans, sarcopterygians and actinopterygians are restricted to specific layers, while placoderms were found in many more horizons of the section and in other parts of the eastern Anti-Atlas (Fig. 4C). The highest abundance and species richness in gnathostomes was found in the phyllocarid layer (middle Famennian corresponding to the *Maeneceras* horizon) containing seven species, whereas only one to two species occurred in the other layers (Fig. 8). In this layer, we found three species of placoderms (*Dunkleosteus,*

*Driscollaspis* sp. nov., and a second undescribed placoderm n. gen. et sp.), chondrichthyans (*Phoebodus* sp., two undescribed cladodonts) and one actinopterygian (work in progress). Approximately 20 m above the phyllocarid layer, remains of cladodont chondrichthyans were found, while the sarcopterygians were found six meter below the *Annulata* Black Shales (Fig. 4C). Further skeletal remains of *Dunkleosteus* occurred in the late middle Famennian strata and a co-occurrence of *Titanichthys* and *Dunkleosteus* was found in layers of late Famennian age. The Hangenberg Black Shale equivalent yielded small teeth of ischnacanthid acanthodians (Klug et al., 2016).

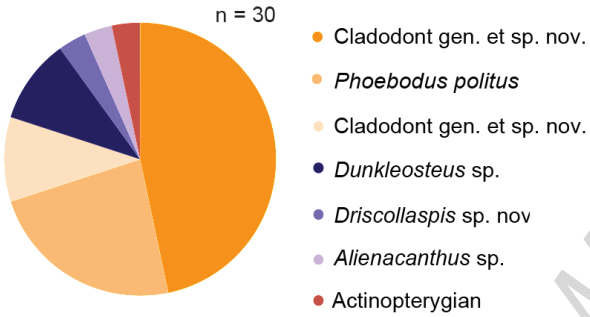


**Fig. 8.** Abundance of different species of Famennian gnathostomes in the phyllocarid layer of the southern Maïder region (northeastern Anti-Atlas, Morocco).

The ecospace use of the gnathostomes of the Maïder Basin is homogenous. Placoderms such as *Dunkleosteus* and *Titanichthys* as well as cladodont chondrichthyans are assumed to have been pelagic animals (Ginter et al., 2010; Carr, 2008, Carr and Jackson, 2008; Long & Trinajstic, 2010). The two additional placoderm species are assumed to have lived in the water column as well because they do not show mouth parts specialized for crushing hard shelled prey. Phoebodont chondrichthyans inhabited a narrower range of environments ("moderately deep to moderately shallow waters"; Ginter et al., 2010). *Onychodus* was reported from the inter-reefal basin of the Gogo Formation (Playford, 1980; Andrews et al., 2006; Long and Trinajstic, 2010) and therefore, the onychodont sarcopterygians of Madène might have been living in the water column as well. Most of these gnathostomes have been

assumed to have been preying on other vertebrates or invertebrates such as phyllocarids, cephalopods as well as conodonts (e.g., Jaekel, 1919; Miles, 1969; Williams, 1990; Mapes et al., 1995, Zatoń et al., 2017). An exception is the placoderm *Titanichthys* that was supposedly a filter feeder because of its long jaw plates with rounded cross section (Denison, 1978).

## 4. Discussion

### 4.1. Invertebrate diversity, ecospace occupation and trophic nuclei during the Famennian

Examination of alpha diversity, taxonomic composition and ecospace occupation shows that environmental conditions at Madène el Mrakib were mostly oxygen-depleted during much of the Famennian. The faunal composition often includes opportunistic species that were tolerant to oxygen depletion (*Guerichia*, buchiolid bivalves, small vetigastropods and bellerophontids, *Chondrites*; Wignall and Simms, 1990; Amler, 1996, 2004) and deep-water species (e.g. the brachiopods *Aulacella* and *Phacoiderhynchus* as well as the bivalve *Loxopteria*; Sartenaer, 2000; Nagel-Myers et al., 2009). Occurrences of pelagic and opportunistic taxa as well as fluctuant environments (several transgressions within a larger regressive cycle) in the Famennian were reported from the Maïder Basin (Becker 1993; Hartenfels and Becker, 2009; Hartenfels, 2011; Hartenfels and Becker, 2016a, b) as well as from localities outside Morocco (Dreesen et al., 1988; Becker and House, 1997; Sandberg et al., 2002; Kaiser et al., 2006; Marynowski et al., 2007; Joachimski et al., 2009; Racka et al., 2010).

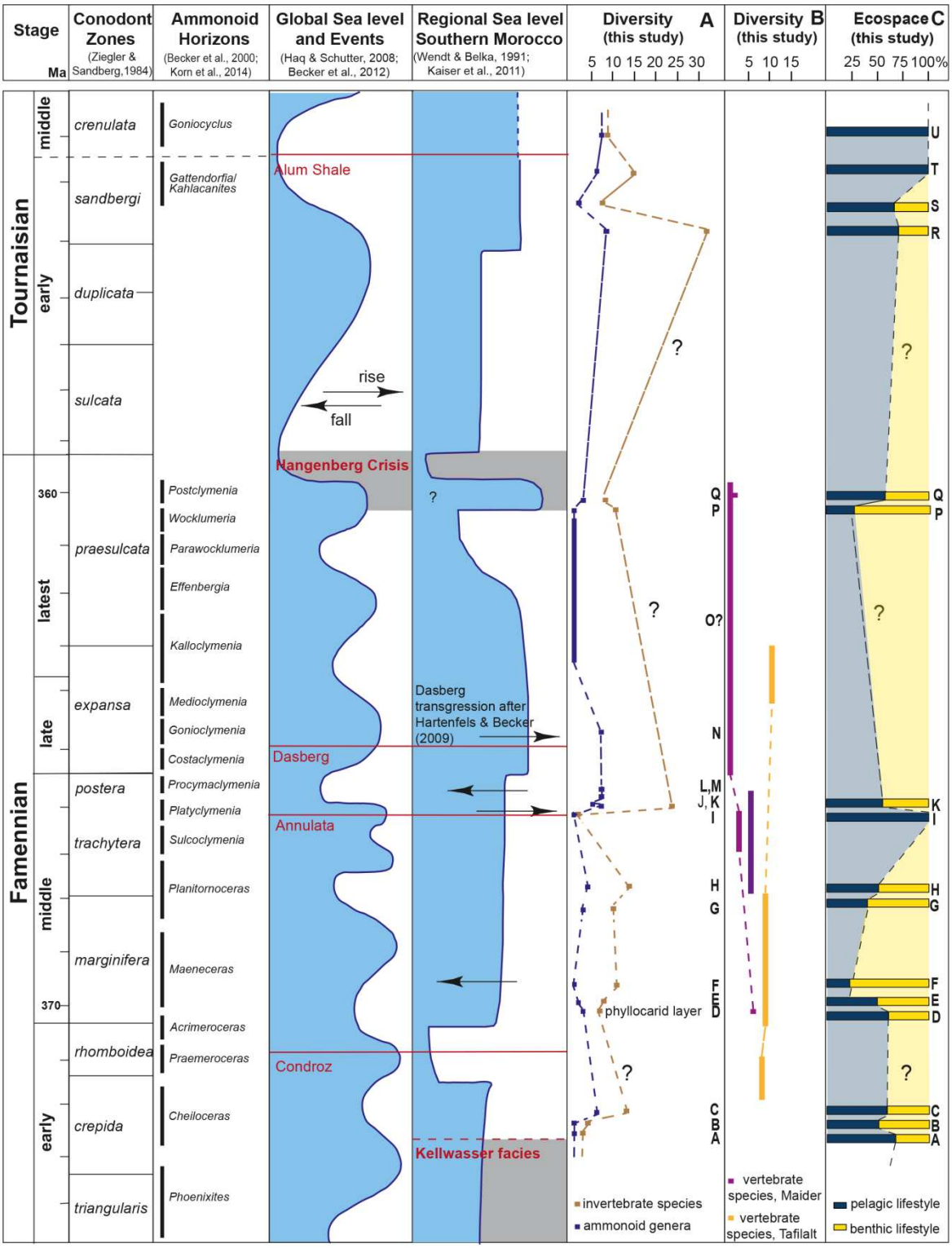


**Fig. 9.** Conodont zones (after Ziegler and Sandberg, 1984), ammonoid horizons (after Becker et al., 2002, Korn et al., 2014) and eustatic sea levels of the Famennian and Early Tournaisian according to Haq and Shutter (2008). Regional sea level is adopted from Wendt and Belka (1991) for the Famennian and from Kaiser et al. (2011) for the Tournaisian. Green arrows mark regional fluctuations proposed by this work here. A – Changes in diversity: invertebrates of Madène el Mrakib and Aguelmous (brown); number of ammonoid genera (blue) B –

Gnathostome diversity of the Maïder (light purple); microremains of the Maïder from Derycke et al. (2008) (dark purple); gnathostomes of the Tafilalt according to Ginter et al. (2002) and Rücklin and Clément (2017) (orange). Exact positions of vertebrate assemblages within the conodont zones are unknown. C – Changes in pelagic-to-benthic lifestyle ratio within ecospace at Madène el Mrakib and Aguelmous. Dashed lines: sufficient samples are missing.

### 4.1.1. Early Famennian

In this time interval at Madène el Mrakib, the predominant presence of brachiopods and the increase in ammonoid diversity can be explained by a regionally high sea level (Wendt and Belka, 1991) (Figs. 4A: associations A-C; 9A-C). Abundant early Famennian rhynchonellid brachiopods were also reported from the East European Platform and they were often flourishing during major transgressions (Sokiran, 2002). Similar associations containing abundant cephalopods and brachiopods were reported from the early Fammenian *Pa. crepida* and *rhomboidea* zones of the Holy Cross Mountains (Racki, 1990). During this time interval, the ecosystem recovered from the Kellwasser Crisis that caused great structural changes within the marine ecosystem (Becker, 1986; Droser et al., 2000). However, oxygen-poor conditions likely persisted from the Frasnian well into the Famennian, as reflected by the widespread Kellwasser Facies characterized by fossiliferous, black bituminous early Famennian limestones and claystones in the Anti-Atlas (Figs. 4, 9; Wendt and Belka, 1991). We did not detect the Condroz event,which coincides with a regression (sea level curves in Fig. 9), perhaps due to insufficient sampling. Probably this interval was covered by scree at Madène el Mrakib (see stratigraphy in Fig. 4).

### 4.1.2. Middle Famennian

During the middle Famennian, species richness varies between six and fourteen species (Fig. 4A, associations A-H) in our samples. The ecospace occupation fluctuates between three

and seven modes of life and the proportion between benthic and pelagic lifestyles is varying (between 33 % and 82 %) in these associations. Changes in the composition of the associations reflect fluctuations in the level of oxygenation at the seafloor, which, in turn, coincide with global rather than regional sea level changes (Fig. 9). For instance, the widest extension of ecospace use (including several benthic lifestyles represented by relatively large and epibenthic bivalves and the contemporary decrease in ammonoid diversity; Figs. 4B, 9C, association F) indicates an increased ventilation of the seafloor that correlates with a global regression (global sea level curve in Fig. 9; Haq and Schutter, 2008; Becker et al., 2012). The faunal signals appear to coincide with eustatic rather than with regional sea-level changes; therefore, we assume that the Famennian sea level of southern Morocco (Wendt and Belka, 1991) is more fluctuant than previously reported by these authors (regional sea level curve in Fig. 9). This is not so surprising when the configuration of the Maïder Basin is taken into account. Towards the northwest and southeast, it was surrounded by land and in the West and East by topographic highs, namely the marine Maïder Platform and the Tafilalt Platform (Wendt, 1985; Kaufmann, 1998). This area of shallower water limited the water exchange between the two basins; this implies a further reduction of water exchange during eustatic sea-level lowstands. By contrast, during lowstands, some areas might have been more oxygenated because wave action reached closer to the sediment surface. Another factor we have not assessed yet is the influence of fresh water from the surrounding land. The existence of rivers is documented by local occurrences of fine clastic sediments and trunks of *Archaeopteris* in the Maïder and Tafilalt Basins (Wendt and Belka, 1991).

#### 4.1.3. Middle Famennian *Annulata* Black Shales

During the deposition of the *Annulata* Black Shales, the ecosystem was depleted with only two species represented by nektonic cephalopods only at Madène el Mrakib. However, 25

species of cephalopods (including seven ammonoid genera) were previously reported from the entire *Platyclymenia* horizon of the Maïder (Korn, 1999; Korn et al., 2014, 2015a, b; Figs. 7: association J; 9A; Table S1). Hartenfels and Becker (2016a) reported some benthic taxa from the Lower *Annulata* Event interval of Mrakib such as small gastropods and guerichid bivalves. The dominance of pelagic taxa in our section of Madène el Mrakib and the possible occurrence of benthos tolerant to oxygen depletion indicates anoxic to dysoxic conditions at the bottom caused by a global transgression (Haq and Schutter, 2008; Hartenfels, 2011; Hartenfels and Becker, 2016a). Anoxic conditions during the deposition of the *Annulata* Black Shales were reported from geochemical analyses of southern Poland as well, although they were interrupted by a better oxygenated phase (Racka et al., 2010). *Annulata* Black Shales with occurrences of pelagic species and the opportunistic bivalve *Guerichia* were reported worldwide (Becker, 1993; Becker and House, 1997; Sanz-López et al., 1999; Becker and House, 2000; Sandberg et al., 2002; Korn, 1999, 2004; Becker et al., 2004; Hartenfels et al., 2009; Hartenfels and Becker, 2016a).

Bio-events do not always strongly affect the ecospace: e.g., the global species richness in bivalves was affected while the ecological diversity stayed stable throughout Earth's history (Mondal and Harries, 2016). However, on the regional scale and including higher time-stratigraphic resolution and different invertebrate groups, ecospace might be more variable. The ecospace use can quickly change as well; for example, the association that follows the *Annulata* Black Shales is quite diverse, thus reflecting a rapid recovery of the biota corresponding to a global and rapid drop of the sea level (22 species including several benthic lifestyles and abundant ammonoids are present; Figs. 4A, 9A, C: association K). The biota recovered faster than after the Kellwasser Crisis, probably because the *Annulata* Event caused less profound ecological changes. Diversity data of the complete invertebrate associations are missing from the overlying middle Famennian interval. However, three ammonoid-based

samples show that at least in this group, no major changes were occurring (five to seven genera are present) and therefore, environmental conditions might have stayed similar.

In the late Fammenian parts of our section at Madène el Mrakib, we did not find any black shales corresponding to the Dasberg Crisis at the transition of the Lower/ Middle *expansa* conodont Zone, although it has been documented from the Maïder Basin (Becker, 1993; Kaiser et al., 2008; Hartenfels and Becker, 2009).

#### 4.1.4. Latest Famennian and Hangenberg Black Shale equivalent

The uppermost Famennian sedimentary succession at Madène el Mrakib is largely covered by the scree of massive sandstone blocks of the Fezzou Formation (Hangenberg Sandstone equivalent). In the scree, we found material of several ammonoid species and only few benthic organisms. Ammonoid samples (benthos is underrepresented with very few specimens of nuculid bivalves, rhynchonellid and chonetid brachiopods as well as crinoids) from Madène el Mrakib do not show any major changes in the *Gonioclymenia* horizon (seven genera are present like in the preceding, i.e., slightly older, late Famennian strata; Korn et al., 2015a; Korn et al., 2016a, b; Table S3). However, only one ammonoid genus is present in the *Kalloclymenia* to *Wocklumeria* horizons of Madène el Mrakib. When comparing collections from other localities in the Maïder (Lambidia, Tourirt and Bou Tlidat), these comprise seven ammonoid genera and therefore, some species might have been missed at Madène el Mrakib due to insufficient sampling effort and the spatial variation of the fossil record.

The associations of Hangenberg Black Shale equivalent contain a higher overall diversity including more benthos represented by bivalves (especially *Guerichia elliptica*) and bryozoans (but possibly as epizoans on ammonoids) as well as bioturbation (small and ubiquitous *Chondrites*) compared with the *Annulata* Black Shales (Figs. 4: associations P-Q; 9C). The abundance of bioturbation indicates that the Hangenberg Black Shale equivalent was

deposited under hypoxic rather than entirely anoxic conditions, or at least with varying levels of oxygen (Klug et al., 2016) at Madène el Mrakib. This finding does not contradict results of geochemical analyses of sections in localities of Morocco and southern Europe that revealed evidence for anoxia during the deposition of the Hangenberg Black Shale (Kaiser, 2005, Kaiser et al., 2006, 2008), because all these benthic organisms (reflected also in the trace fossils) were likely tolerant towards low oxygen levels at the sea-floor. Sea-level curves for the Devonian of Morocco show a transgression during the deposition of the Hangenberg Black Shales followed by a regression in the overlying Hangenberg Sandstone equivalent (Kaiser, 2005; Kaiser et al., 2011, 2015). Similarly, the global sea level curve shows a transgression followed by a regression during the Hangenberg Crisis (Haq and Schutter, 2008).

#### 4.1.5. Early and middle Tournaisian

During the early to middle Tournaisian of Aguelmous, nektonic cephalopods were flourishing while benthic organisms were rare (bivalves, tabulate and rugose corals, gastropods, bellerophontids, brachiopods, spiriferids; Fig. 6, Table S3, association R-U) with some exceptions in the Maïder and Tafilalt. This is reflected in the scarcity of strata with abundant bioturbation, but this might be a wrong impression rooting in the fact that the fine-grained siliciclastic sediments (claystones, siltstones and fine-grained sandstones) are deeply weathered and often covered by scree (personal observation by CK). However, the samples are biased (sampling) towards ammonoids what is reflected by the almost parallel curves of the ammonoid genera and total species richness. Haq and Schutter (2008) reported a sea-level rise followed by a drop in the *sandbergi* Zone which could have decreased the ammonoid diversity at Aguelmous. But the regional sea level (Bou Tlidat, Kaiser et al., 2011) remained high during this interval and from several localities of the Tafilalt, a second eustatic

transgression was reported (Lower Alum Shale Event, early/ middle Tournaisian boundary; *crenulata* biozone), that favored pelagic life (Kaiser et al., 2008, 2011, 2015). The Lower Alum Shale Event caused extinction in several groups, however in ammonoids probably only at species level (Kaiser et al., 2011, 2015; see ammonoid record in Ebbighausen and Bockwinkel, 2007).

**4.2. Diversity and palaeoecology of gnathostomes**

Similar to the invertebrates, the Famennian vertebrate diversity of the Maïder Basin was depleted (placoderms: *Dunkleosteus*, *Titanichthys*, *Driscollaspis* sp. nov., an undescribed placoderm; chondrichthyans: *Phoebodus* sp., two undescribed cladodonts; sarcopterygian: Onychodontidae; actinopterygian: aff. *Moythomasia*) (Figs. 4C, 8, 9B). Previously reported microremains of chondrichthyans from the middle Famennian (*Palmatolepis trachytera* and *Pa. postera* zones) of the Maïder include similar faunal components (*Thrinacodus tranquillus*, *Stethacanthus,* possibly *Cobelodus*, *Denaea*, undetermined cladodonts) and pointed at a low diversity as well (Derycke et al., 2008; Derycke, 2014, 2017). The pelagic and highly to moderately mobile predators (except for the supposedly filter feeding placoderm *Titanichthys*) preferably preyed on other pelagic organisms such as cephalopods, fishes and phyllocarids (Williams, 1990; Mapes et al., 1995) this might explain the high abundance of gnathostomes (especially chondrichthyans: 23 individuals) in the phyllocarid layer. A co-occurrence of crustaceans and gnathostomes is known from Frasnian rocks of the Gogo-Formation of Australia (Briggs et al., 2011) as well as the Cleveland Shale in the USA (Williams, 1990) and indicates that crustaceans could have been a nutritive food source for early vertebrates. However, it has to be considered that the preservational probability was higher in these layers at these localities as even small phyllocarids have been preserved. The deposition of the Moroccan phyllocarid layer coincides with a global regressive cycle showing that the

gnathostome preferred an environment that was shallower and better ventilated. However, when compared to the regional sea-level curve (Fig. 9B), these correlations are not evident.

Gnathostome abundance and diversity is much lower (one to two species of placoderms) in the upper parts of the middle and upper Famennian sedimentary rocks where cephalopods and brachiopods are most common. Last occurrences of vertebrates, namely two teeth of ischnacanthid acanthodians, were found in the Hangenberg Black Shale equivalent of Madène el Mrakib, although the potential for the preservation of vertebrate macroremains is high in these shales (Klug et al., 2016). Nevertheless, the upper Famennian rocks (*Pa. expansa* Zone) of the adjacent Tafilalt region (northeastern Anti-Atlas, Morocco) are rich in gnathostome microremains (Ginter et al., 2002). Generally, the middle and upper Famennian carbonates of the Tafilalt region are more diverse compared to the Maïder Basin in yielding about 17 pelagic and benthic species of the chondrichthyan genera *Jalodus*, *Thrinacodus*, *Phoebodus*, *Ctenacanthus*, *Stethacanthus*, *Symmorium*, *Cobelodus*, *Denaea*, *Protacrodus*, *Siamodus*, *Clairina* (Derycke, 1992, 2017; Ginter et al., 2002). There is a clear difference in preservation of cartilaginous fishes: more or less complete skeletons in the Maïder versus exclusively microremains in the Tafilalt. These differences in gnathostome ecology, diversity and preservation likely resulted from different environmental conditions between the two regions. The Maïder Basin was deeper than the Tafilalt pelagic ridge and the western part of the Tafilalt Basin and was isolated from the open ocean by land and shallow marine areas (Wendt, 1985, 1995; Wendt et al., 2006; Fröhlich, 2004; Lubeseder et al., 2010) and therefore, the Maïder Basin and especially its bottom waters were not well ventilated at all times. These conditions could explain the poor diversity in invertebrates (especially benthos) and vertebrates. Additionally, this partially explains the preservation of articulated vertebrate skeletons as strong currents and scavengers were rare or absent close to the sediment surface.

In the Tournaisian (Early Carboniferous), neither the Maïder nor the Tafilalt was rich in vertebrates. This is in accordance with the global fossil record of vertebrates. With a few

exceptions (Alekseev et al., 1994), early Tournaisian vertebrates are globally rare and even the extremely diverse late Famennian gnathostome fauna of the Cleveland Shales vanished entirely (Hansen, 1996; Friedman and Sallan, 2012). Environmental perturbations during the late Famennian might have strongly affected the ecosystem but the environment in the Tournaisian itself was probably not suitable for a diverse gnathostome ecosystem. Living conditions were probably suitable for some pelagic but not for benthic gnathostomes due to high sea levels, and an environment dominated by pelagic cephalopods.

It has to be considered that the biota reacted not only to abiotic but indirectly also to biotic changes. Biotic factors as causes for changes in ancient ecosystem are often dismissed because direct evidence of botic interactions (e.g. stomach contents) are rarely preserved (Williams, 1990; Martill et al., 1994; Cavin, 1996; Richter and Baszio, 2001; McAllister, 2003; Kriwet et al., 2008; Sallan et al., 2011; Zatón et al., 2017; Chevrinais et al., 2017). In the case of the Famennian and Tournaisian of the Maïder, prevailing anoxic to dysoxic conditions at the seafloor likely limited benthonic life (primary consumers), important food source for small fishes (secondary consumers), which, in turn, represent prey for bigger fishes such as predatory placoderms and chondrichthyans (third level consumers). Moreover, the missing predation pressure by gnathostomes on the ammonoids during the early Tournaisian might have fostered the rapid re-diversification of ammonoid taxa. Patterns like this were described from early Carboniferous crinoids that diversified after the extinction of their predators (Sallan et al., 2011). However, work on higher stratigraphic resolution and comparisons among different localities have to be carried out in order to test the assumed relationship between extinction of predators and a subsequent radiation of ammonoids. Moreover it is hardly assessable to what extend regional migration patterns influenced the biota of the Maïder and therefore, if the regional diversity and ecological trends can be fully assigned to the global ecosystem.

## 5. Conclusions

Quantitative analyses of 21 invertebrate associations from the Famennian to middle Tournaisian sedimentary rocks of the Maïder Basin document an ecosystem mostly dominated by pelagic invertebrates (particularly cephalopods) and gnathostomes (phoebodont and cladodont chondrichthyans, placoderm such as *Dunkleosteus* and *Titanichthys*). The ecospace extension of invertebrates reacted to eustatic and/ or regional sea-level changes that caused fluctuations in ventilation and thus, oxygenation of the seafloor. Based on the variable occurrence of benthic lifestyles, we propose that changes in regional sea-level and their effects were stronger than previously thought; this applies in particular to the beginning of the middle Famennian and around the *Annulata* Black Shales. A fluctuating sea level is also supported by changes in sedimentological composition (alternating clay, marls and nodular limestone) in the Maïder.

Reduction of ecospace occupation (especially in benthic lifestyles) occurred after and during bio-events: The slightly recovered biota after the Kellwasser crises was strongly affected during the late Famennian, which is reflected in a low ecological diversity (two modes of life) during the deposition of the *Annulata* Black Shales. Although the biota recovered rapidly from this bio-event (seven modes of life), the ecological diversity declined again during the *Wocklumeria* horizon and the Hangenberg Crisis (five and two modes of life). The biota did not recover very quickly from these crises and ecological depletion persisted during the early Tournaisian.

Attention should not solely be paid to big events (Kellwasser and Hangenberg crises) but also to small-scale environmental changes (e.g. Condroz, *Annulata* and Dasberg events) as well as other environmental and ecological changes during the Famennian. Unstable biota fluctuating in numbers of species and modes of life might have been affected even more

strongly by mass-extinctions than biota in stable ecosystems. It is hardly assessable how the changes in environmental conditions and invertebrate ecology affected the accompanying vertebrates due to the comparably low diversity and abundance of gnathostomes in the Maïder Basin (except for the phyllocarid layer where phyllocarids were abundant and likely a suitable prey). Nevertheless, biotic interactions are probable and strong fluctuations in the abundance and diversity of primary consumers (invertebrates) disturbed the local food web and represent the likely explanation for the limited abundance and diversity of secondary and third level consumers (gnathostomes). In order to obtain more information about the impact of small-scale events and environmental changes on regional and global biota of the end-Devonian, it is necessary to examine ecospace occupation of invertebrates as well as vertebrates in other localities during this time interval.

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## Highlights

- Ecospace of invertebrates reacted to Famennian bioevents and sea level fluctuations
- Palaeoecology of the fauna indicates oxygen-depleted conditions at the sea floor
- Abiotic and biotic changes might have influenced Famennian vertebrate diversity